BATS REFERRED TO *HESPEROPTENUS* PETERS, 1869 (CHIROPTERA : VESPERTILIONIDAE) WITH THE DESCRIPTION OF A NEW SUBGENUS

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BATS REFERRED TO *HESPEROPTENUS* PETERS, 1869 (CHIROPTERA: VESPERTILIONIDAE) WITH THE DESCRIPTION OF A NEW SUBGENUS

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CONTENTS

SYNOPSIS

Species currently allocated to the vespertilionid genus *Hesperoptenus* are reviewed in detail and divided into two subgenera, one, *Hesperoptenus* (*Milithronycteris*) with type species *Nyctice-jus tickelli* Blyth, 1851, proposed as new, to include also *H. blanfordi* (Dobson, 1877) and *H. tomesi* Thomas, 1905. The nominate subgenus contains only its type species *H. doriae* (Peters, 1869), here reported for the first time from Malaya, this being the second record of the species, hitherto known only from its holotype from Sarawak, Borneo.

INTRODUCTION

BATS of the Asiatic genus *Hesperoptenus* are, in general, rarely collected and therefore do not feature extensively in museum collections. Consequently, they remain for the most part rather poorly known and, apart from one Indian species, have received only scant attention in the literature. As it is currently recognized, *Hesperoptenus* is held to include four species, *doriae*, *tickelli*, *tomesi* and *blanfordi*. Their association together has been considered open to doubt by some authors while the most recent definition of the genus is based upon *tickelli* rather than upon the type species *doriae*. In this account the four species are examined and compared and although the number of specimens available remains small in some it has been possible nevertheless to describe the features of each species in detail and to discuss their differences and possible relationships. As a result, *Hesperoptenus* as previously understood is divided into two subgenera, one described as new.

HISTORY

The name *Hesperoptenus* was proposed by Peters (1869a : 626) for a subgenus of *Vesperus*, with type species *V.* (*H.*) *doriae* described concurrently from Sarawak, Borneo. Shortly afterwards, Peters (1869b : 638) described *V.* (*H.*) *kraussi* from Yoruba, Lagos, Nigeria, nowadays considered a synonym of *Glauconycteris poensis* (Dobson, 1878 : 255 ; Thomas, 1913 : 145 ; Rosevear, 1965 : 275). The two species described by Peters are figured together in his posthumous publication of illustrations of Chiroptera from the Zoologische Museum, Berlin (1906, pl. 26), and in this are referred to *Vesperus*, with no mention of *Hesperoptenus*.

Dobson (1876 : 112) in a monographic study of the Asiatic Chiroptera placed *doriae* in the genus *Vesperugo*, largely repeating the description by Peters, in translation. Dobson remarked that he thought *doriae* to be closely allied to *Vesperugo tickelli* (Blyth, 1851) and that when specimens of both could be compared it would be found that they could be included together in the subgenus *Hesperoptenus*. Later, Dobson (1877 : 312) described *Vesperugo* (*Hesperoptenus*) *blanfordi* and so implicitly recognized *Hesperoptenus* as a subgenus. Subsequently, he (1878 : 239) defined *Hesperoptenus* as a subgenus of *Vesperugo*, to include *doriae*, *tickelli* and *blanfordi*. In the same work (p. 255) Dobson reduced *Vesperus* (*Hesperoptenus*) *kraussi* Peters, 1869 to the synonymy of *Glauconycteris poensis*, where it has since remained. Eventually, *Hesperoptenus* as understood by Dobson was raised to generic rank (Jentink, 1887 : 278 ; 1888 : 182 ; Wroughton, 1897 : 723 ; Trouessart, 1897 : 116 ; 1904 : 83), with Thomas (1905 : 575) describing a fourth species, *tomesi*.

The essentials of the classification proposed by Dobson have persisted until the present day. Miller, the monographer of bat genera, retained (1907 : 211) generic rank for *Hesperoptenus* but examined only *tickelli*, which he employed as the basis for his generic diagnosis. This definition moved from the concept established by Dobson (1878 : 239), who, following Peters, had characterized the subgenus *Hesperoptenus* by 'outer upper incisors very small, scarcely raised above the gum, generally posterior to the toothrow ; penis with a distinct bone ; post-calcaneal lobe well-developed ; wings from the base of the toes'. Dobson had not seen *doriae* which he stated differed from *tickelli* and *blanfordi* in that the outer upper incisors were in the toothrow and not posterior to it as in these species. Miller (1907 : 211) diagnosed *Hesperoptenus* almost entirely by the features of the dentition, relying largely on the configuration and position of the upper incisors. Since, like Dobson, Miller did not examine *doriae*, he employed *Hesperoptenus* with some hesitation, considering that the description of *doriae* by Peters indicated certain features suggesting that it might be generically distinct from both *tickelli* and *blanfordi*. Miller did note, however, that peculiarities of the prepuce and the presence of a large bone in the penis might indicate (as Dobson had thought with regard to the os penis or baculum alone) that the three species formed a distinct group (Miller did not include *tomesi*, of which he appears to have been unaware) but remarked that the value of these characters was not then well understood.

More recently, Tate (1942 : 268) considered Miller correct in the supposition that more than one genus was involved, but was unable to study either *doriae* or *blanfordi*.

This author referred to the position of the outer upper incisor in *doriae* and suggested further that the specialized thumb of *blanfordi* might be an indication that it too differed widely from its supposed congeners. Ellerman & Morrison-Scott (1951 : 174), who drew attention to this situation, pointed out that the holotype of *doriae* apparently remained unexamined and that the genus *Hesperoptenus* might prove untenable in the sense in which it was then accepted. Davis (1962 : 42) referred a specimen from Sabah, Borneo, to *doriae*, noting that in this example the outer upper incisor was displaced posteriorly. This circumstance led Medway (1965 : 65) to consider that the type species thus conformed to the current generic definition, thereby rendering groundless the speculation by Ellerman & Morrison-Scott. The example from Sabah, however, does not represent the type species but instead should be referred to *tomesi*, of which it is a juvenile male (Hill, 1972 : 38 ; vide infra).

It is clear that the taxonomy of *Hesperoptenus*, so far unresolved, can be clarified only by the detailed examination of the holotype of *doriae*, upon which any interpretation of the genus must turn. The original description by Peters and a brief note of forearm length, colour and incisive dentition by Hill (1972 : 38) appear to be the only published accounts based upon direct examination of the holotype, which is in the Museo Civico di Storia Naturale 'Giacomo Doria', Genoa. This specimen, until recently the only definitively known example of the species, was examined also by Oldfield Thomas, who, in a copy of Dobson's *Catalogue of the Chiroptera in the Collection of the British Museum*, 1878, now in the Library of the British Museum (Natural History), has annotated the remark 'Specimen sent over 12/1901' to the account of *doriae*. Thomas has added manuscript notes on the external features, baculum and incisive dentition, with some measurements, to the account by Dobson. Shortly after the holotype was studied during the early preparation of this paper, a second specimen of *doriae* was obtained quite by chance in Malaya by Lord Medway, almost exactly one hundred years after Peters first acknowledged the species.

Genus ***HESPEROPTENUS*** Peters, 1869

Hesperoptenus Peters, 1869a : 626 (as a subgenus of *Vesperus*). Type species *Vesperus* (*Hesperoptenus*) *doriae* Peters, 1869, from Sarawak, Borneo.

Diagnosis. Similar to *Eptesicus* but differing from this genus in relatively wider palate with wide anterior emargination ; in the presence of well-developed basioccipital pits ; in larger, caniniform inner upper incisor (i^2), its basal area equal almost to one half that of the upper canine (c^1) ; and by the structure of the outer upper incisor (i^3) which is low, its tip reaching barely to the cingulum of i^2 or of c^1, with basin-like cingulum and low central cusp. Dentally similar to *Glauconycteris* but differing from this genus and from the closely related *Chalinolobus* in having the posterior margin of the ear terminating on the head at a point not much anterior to the insertion of the anterior margin, not extending almost to the corner of the mouth, and in the absence of a fleshy lappet on the lower lip near this point. The majority of species of *Hesperoptenus* differ further from *Eptesicus*, *Glauconycteris* and *Chalinolobus* in the marked inward displacement of i^3 from the toothrow.

DESCRIPTION. Muzzle low and wide, sparsely furred anteriorly ; narial openings semi-lunate or nearly circular, opening sub-laterally ; usually a small wart-like protuberance above the anterior canthus of the eye, bearing a few long whiskers ; lower lip with broad median pad ; a small naked or nearly naked area immediately beneath the symphysis menti, preceding a low wart which bears a few long hairs. Ear subquadrangular ; anterior margin with rounded or very slightly pointed posteriorly directed basal lobe ; tip of ear rounded ; posterior margin with prominently developed antitragal lobe effecting a quadrate junction with the side of the head behind and level with the angle of the mouth, from which it is separated by a low wart bearing a few longer hairs. Tragus slightly hatchet-shaped, its upper part prolonged anteriorly. Metacarpals of third, fourth and fifth digits nearly equal in length, the third usually very slightly the longest ; a well-developed post-calcarial lobe, sometimes supported by a cartilaginous spur ; penis with wide, saccular prepuce with large terminal opening.

Skull with wide braincase, the frontal region not especially inflated ; rostrum short ; palate short, wide, the lateral margins of the pre-palatal emargination not extending greatly beyond the inner margins of the inner upper incisors (i^{2-2}) and separated from the canines (c^{1-1}) by a relatively wide ledge of bone ; evident basioccipital pits. Dental formula $i\frac{2}{3}$, $c\frac{1}{1}$, $pm\frac{1}{2}$, $m\frac{3}{3} = 32$; inner upper incisor (i^2) massive, caniniform, unicuspid, with prominent cingulum, the tips of the inner incisors inwardly directed and slightly convergent ; outer upper incisor (i^3) low, with basin-like cingulum from which arises a small pyramidal cusp, extending barely to the cingulum either of i^2 or of the upper canine (c^1) in height ; i^3 sometimes displaced inwardly from the toothrow to the extent that it may lie behind or almost behind i^2 ; third upper molar (m^3) reduced but retaining mesostyle, metacone and three commissures ; third lower molar (m_3) usually only slightly reduced, its posterior triangle a little smaller than its anterior triangle, but considerably so in one species.

DISTRIBUTION. The genus is distributed through India, Sri Lanka, Burma and the Andaman Islands to Thailand and Malaysia, including Borneo.

Subgenus *HESPEROPTENUS* Peters, 1869

DIAGNOSIS. Ear and tragus membranaceous ; second phalange of third digit markedly longer than first phalange ; braincase slightly inflated, rather globose ; rostrum not especially widened ; supraorbital region only very slightly inflated ; lower maxillary margin of orbit narrow, forming a narrow, tapering ledge alongside the toothrow ; maxillary toothrows nearly parallel ; outer upper incisor (i^3) in toothrow or nearly so, not markedly intruded.

DISTRIBUTION AND SPECIES. The subgenus is known so far only from Malaysia and includes solely the species *Hesperoptenus doriae* (Peters, 1869), described originally from Sarawak, Borneo, and here reported for the first time from Malaya.

Hesperoptenus doriae (Peters, 1869)

Vesperus (*Hesperoptenus*) *doriae* Peters, 1869a : 626. Sarawak, Borneo.
Vesperugo (*Vesperus*) *doriae*, Dobson, 1876 : 104, 122.
Vesperugo (*Hesperoptenus*) *doriae*, Dobson, 1878 : 239.
Vesperugo doriae, Dobson, 1880 : 187 ; Hose, 1893 : 40.
Vesperugo donriae Hose, 1893 : 40. Lapsus.
Hesperoptenus doriae, Trouessart, 1897 : 116 ; 1904 : 83 ; Miller, 1907 : 211 ; Chasen, 1940 : 52 ; Tate, 1942 : 269 ; Ellerman & Morrison-Scott, 1951 : 174 ; Davis, 1962 : 42 (erratum, based on *tomesi*) ; Medway, 1965 : 65 (erratum, based on *tomesi*) ; Hill, 1972 : 38.

HOLOTYPE. Adult male CE 40094 in the Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy. In alcohol, skull removed.

DESCRIPTION. Muzzle with a shallow longitudinal groove immediately behind the widely separated narial openings which are nearly circular ; a few sparse hairs along the upper lip between the nostrils, the internarial region otherwise nearly naked and with only a sparse covering of short hairs above the nostrils and internarial pad ; prominent wart above anterior canthus of eye, bearing a few long whiskers ; lower lip with a broad median pad with no more than a trace of a median dividing groove at its posterior border only ; a small naked area beneath the symphysis menti, preceding a low wart which bears a few long hairs. Ears (Pl. 1) membranaceous, not thick or fleshy, rounded, more or less subquadrangular, the external surface of the conch quite densely clothed with hair for about one half the length of the ear, a few sparse hairs on the inner surface ; anterior margin of ear strongly convex, with rounded, posteriorly directed lobe at its base ; tip rounded ; posterior margin shallowly concave distally but otherwise strongly convex ; well-developed, fleshy antitragal lobe thickened along its outer margin, terminating quadrately behind and level with the corner of the mouth but separated from it by a low wart bearing a tuft of longer hairs. Tragus (Figs 1a, 1b ; Pl. 1) membranaceous, about one half the length of the ear, its anterior margin straight proximally, concave distally ; tip rounded, directed anteriorly ; upper margin nearly horizontal, sloping only slightly posteriorly, curving convexly to the slightly convex posterior margin which has a large, more or less triangular lobe at its base.

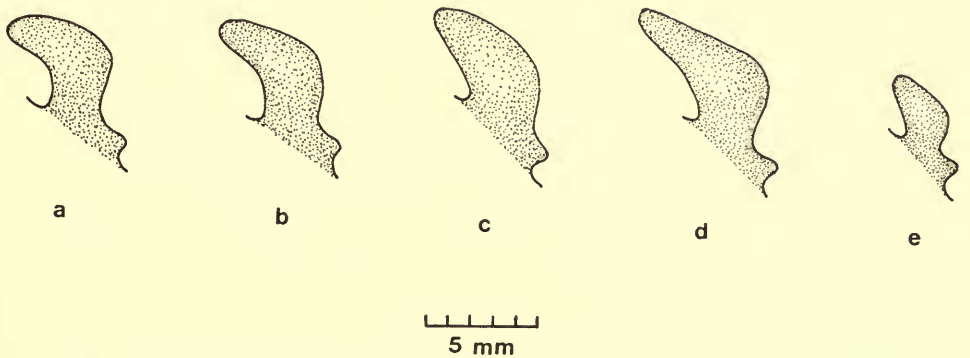

FIG. 1. Tragus of : (a) *Hesperoptenus doriae*, holotype, Sarawak ; (b) *H. doriae*, Malaya ; (c) *H. tickelli* ; (d) *H. tomesi* ; (e) *H. blanfordi*.

Thumb long, its upper surface sparsely haired, with a strong claw ; forearm naked except for a few hairs proximally ; upper surface of tibia and of toes with a few scattered hairs ; fur extending sparsely on to the dorsal surface of the uropatagium for about one half its width, the ventral surface similarly but more thinly haired. Third metacarpal the longest, second and fourth very slightly shorter, the fifth the shortest ; second phalange of third digit longer than first phalange ; endopatagium and uropatagium slightly reticulated, remainder of flight membrane striated ; a rounded post-calcarial lobe supported by a poorly defined cartilaginous prop ; penis with saccular prepuce, sparsely haired, with V-shaped preputial opening. Holotype dorsally pale brown, hairs dark brown at the base but pale straw for much of their length, the ventral surface similar but paler, the specimen evidently much bleached by long immersion in alcohol. A second specimen (in alcohol) from Malaya is dark brown above and below, the membranes blackish brown.

Skull (Pl. 1) small, with inflated, slightly globose braincase, more elevated posteriorly than anteriorly, the frontal region slightly inflated ; slight lambdoid crests ; postorbital region sharply constricted ; rostrum short, narrow, with very slight supraorbital ridges, the supraorbital region only very slightly inflated ; a shallow depressed area immediately above anteorbital foramen ; anterior margin of orbit in frontal aspect sloping slightly inwards towards upper surface of rostrum ; shallow median rostral depression. Narial emargination wide, deep, extending posteriorly to a line joining the anterior edges of the anteorbital foramina, in the holotype V-shaped, with rounded apex, in a Malayan specimen U-shaped.

Zygomata slender ; anteorbital foramen closed by a narrow bar of bone ; lower maxillary margin of orbit narrow, not especially flange-like ; pre-palatal emargination wide, extending laterally a little beyond the inner faces of the inner upper incisors (i^{2-2}) and posteriorly to a line joining the posterior faces of the canines (c^{1-1}), rounded posteriorly, its lateral margins forming a narrow bony shelf. Palate rather short and wide, the maxillary toothrows nearly parallel ; post-palatal extension long, its lateral margins initially more or less parallel, with a slight convex expansion a little more than halfway along the extension, the margins then convergent, the hamulars convergent posteriorly ; post-palatal spine prominent, broad at the base. Soft palate (Fig. 2a) with five post-canine ridges, the first unbroken, the remainder each medianly divided, curved convexly on each side of the palate towards its centre. Basioccipital narrow, with deep, narrow basioccipital pits, separated by a narrow ridge, the bullae relatively large.

Baculum (Fig. 3a) of holotype damaged, but has evidently a long, relatively wide, flattened shaft with little sign of any pronounced upward curvature. At the base the baculum is expanded to form paired basal flanges, thick and massive, separated above and below by shallow median fissures. The shaft itself is parallel-sided ; in section its upper surface is slightly convex, the ventral surface in the proximal and central parts of the shaft slightly concave. Towards the tip the shaft is thickened vertically, the tip itself rounded

Inner upper incisor (i^2) caniniform, large, unicuspid, its basal area one half that of the upper canine (c^1), with prominent cingulum. Anterior face rounded, tooth with slight lateral edges, postero-lateral faces scooped out at each side of a posterior

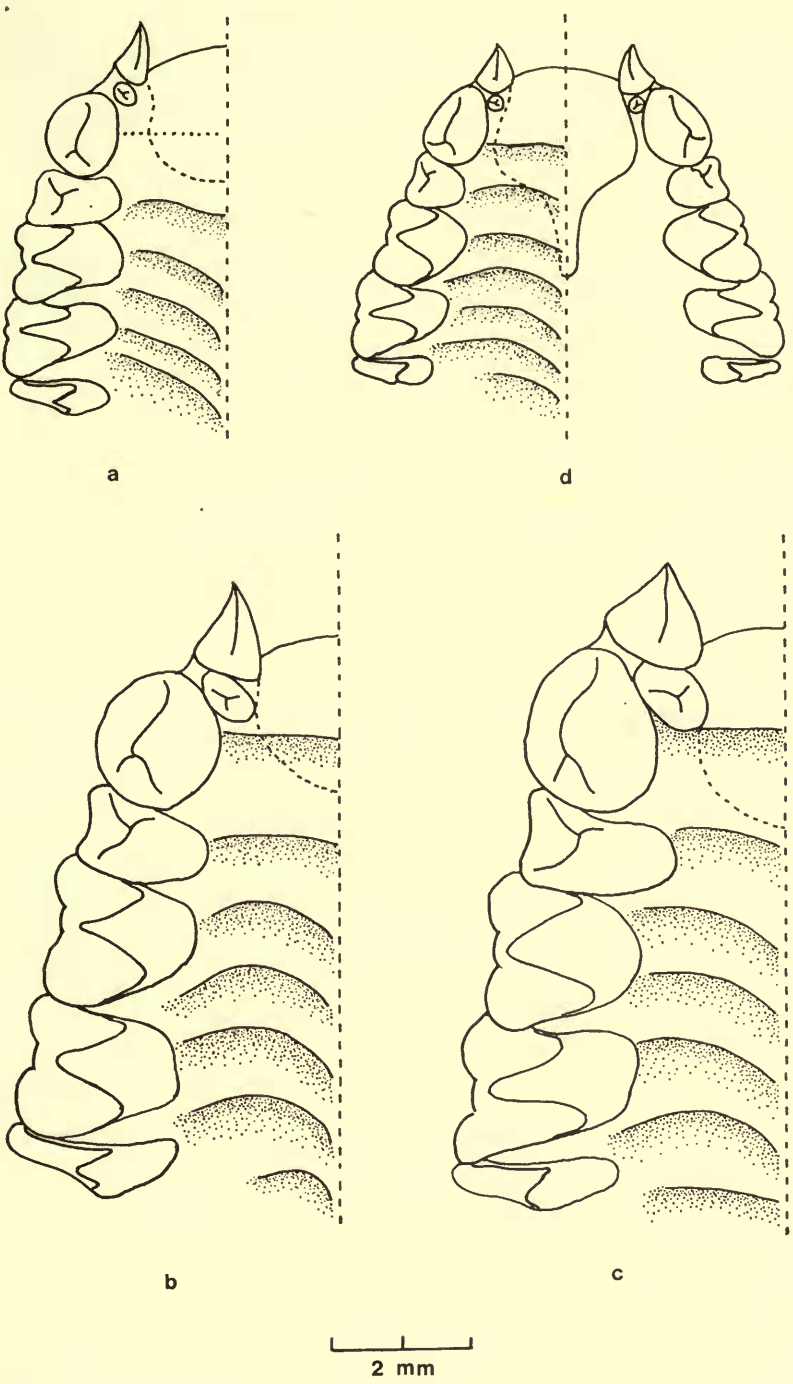

FIG. 2. Palate ridges of : (a) *Hesperoptenus doriae*, Malaya ; (b) *H. tickelli* ; (c) *H. tomesi* ; (d) *H. blanfordi*.

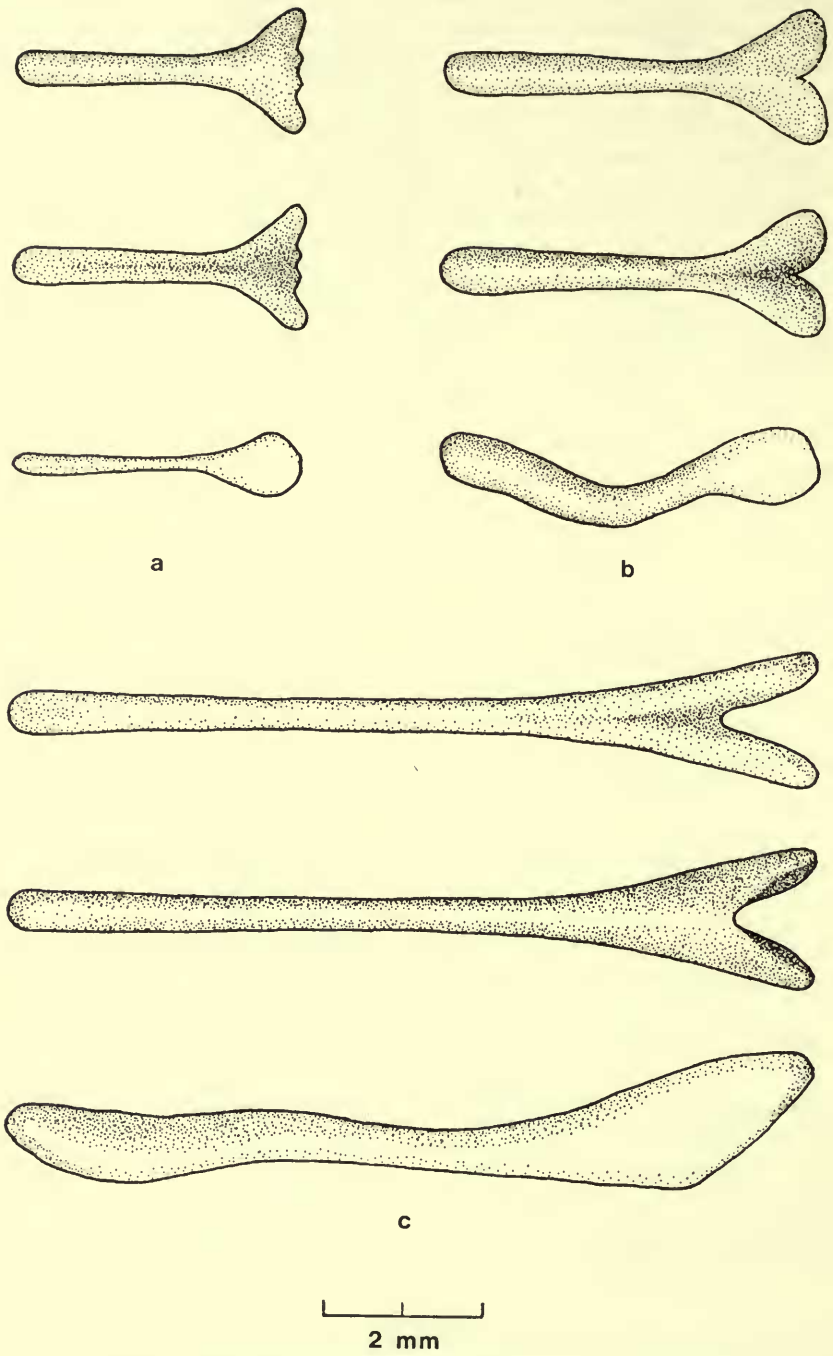

FIG. 3. Baculum of : (a) *Hesperoptenus doriae*, holotype ; (b) *H. tickelli* ; (c) *H. tomesi*, holotype.

median knife-like ridge. Outer upper incisor (i^3) simple, basal area little more than one quarter that of i^2, with basin-like cingulum and simple central cusp, i^3 basally slightly ovate, the longer axis lying diagonally to the toothrow; not displaced or only very slightly intruded, in contact or nearly so with i^2 and c^1, which is massive, with small anterior and posterior cingulum cusps. Upper premolar (pm^4) twice as wide as long, not compressed in the toothrow: first and second upper molars (m^{1-2}) with low hypocones, their lingual margins rounded; third upper molar (m^3) about one half crown area of m^1, with metacone and three commissures, the third not greatly reduced. Lower incisors (i_{1-3}) tricuspid, linear, slightly imbricated, i_3 a little thickened; anterior lower premolar (pm_2) about one third the crown area of the second lower premolar (pm_4); entoconid and hypoconid of third lower molar (m_3) not greatly reduced, one half the height of the anterior cusps, the tooth only slightly narrowed posteriorly (Pls 2 and 4d).

Measurements of the holotype and of a female example from Malaya appear in Tables 1 and 2.

Distribution. Malaya (Selangor); Borneo (Sarawak). *Hesperoptenus doriae* is known apparently only from the holotype from Sarawak and from a female example (in alcohol, skull extracted) obtained by Lord Medway on 14 February 1969 at the Field Studies Centre, Ulu Gombok, Selangor, Malaya. This further specimen is now in the collections of the British Museum (Natural History). No direct comparison with the holotype has been possible but as far as can be determined the two specimens are in close agreement except for the more rounded, less angular narial emargination of the Malayan example.

Remarks. The inflated, slightly globose braincase of *H. doriae* removes it rather sharply from *Eptesicus* and suggests *Glauconycteris* or the closely allied *Chalinolobus*, which are thought to be subgenerically related by Ryan (1966 : 86, 89) and by Koopman (1971 : 1). However, these differ from *Hesperoptenus* in the insertion of the posterior margin of the ear and in the presence of a lappet on the lower lip near the angle of the mouth, and the rostrum in general is more shortened. Externally, *H. doriae* is strongly reminiscent of *Eptesicus* or *Pipistrellus* and indeed its baculum is of the long-shafted type associated with the latter genus. Dentally, the species has some features in common with *Glauconycteris* in which the outer upper incisor (i^3) has a wide cingulum with simple central cusp and stands in the toothrow, although in some species a small degree of extrusion is found, to approach the condition usual in *Chalinolobus* in which the four upper incisors lie on a line in most species. In *H. doriae* the tendency is for i^3, although in the toothrow, to lie towards its inner or lingual border: the inner margins of the inner upper incisor (i^2), of i^3 and of the upper canine (c^1) lie on a line, with the outer margins of i^2 and c^1 extending considerably beyond the outer margin of i^3. Although on occasion a similar situation occurs in *Glauconycteris* (cf. *G. gleni*, vide Peterson & Smith, 1973 : 3, fig. 2, centre) the tendency in this genus seems to be for i^3 to become extruded. *Hesperoptenus doriae* differs further from *Glauconycteris* in its rounded and not linear postcalcarial lobe and in having the second and third lower incisors (i_{2-3}) linear and imbricated, lacking any low posterior cusp, rather than standing along the line of the

TABLE 1

External measurements (in mm) of *Hesperoptenus*

	H. doriae		*H. tickelli*			*H. tomesi*			*H. blanfordi*		
	Holotype ♂, Genoa Museum CE 40094 Sarawak	♀, BM 75.1873 Malaya	n	Range	Mean	Holotype ♂, BM 7.1.1.428 Malaya	♂, BM 74.455 Malaya	♀, BM 74.456 Malaya	n	Range	Mean
Length of forearm	38·0	41·1	44	49·1–60·3	54·0	51·0†	50·3	51·2	6	25·2–28·4	26·6
Length of thumb (with claw)	8·1	8·3	6	12·1–13·2	12·9*	11·5†	11·8	12·0	3	4·0– 4·3	4·2
Length of II^m	35·9	39·4	6	47·3–54·1	49·4*	45·0†	46·4	45·9	3	24·0–24·4	24·2
Length of III^m	36·8	39·5	6	48·0–53·6	50·1*	47·3†	47·8	47·2	3	25·2–26·3	25·7
Length of III^1	15·6	17·8	6	21·1–25·0	22·4*	21·9†	22·5	23·0	3	13·1–15·0	13·8
Length of III^2	19·0	21·3	6	21·8–25·0	22·8*	15·8†	16·8	16·5	3	8·0– 9·1	8·6
Length of IV^m	36·0	38·3	6	47·6–51·8	49·5*	47·3†	47·7	46·8	3	24·3–26·3	25·4
Length of V^m	34·8	36·8	6	47·3–52·0	48·9*	44·0†	44·1	44·6	3	23·2–25·4	24·4

n, number of specimens.
* Specimens from Sri Lanka only: no Indian examples in alcohol available.
† From dry skin.
The nomenclature for the digits in this table and in Table 3 follows a convention where, for example, III^m is the metacarpal of the third digit, III^1 and III^2 its first and second phalanges.

TABLE 2

Cranial measurements (in mm) of *Hesperoptenus*

	H. doriae		*H. tickelli*			*H. tomesi*			*H. blanfordi*		
	Holotype ♂, Genoa Museum CE 40094 Sarawak	♀, BM 75.1873 Malaya	n	Range	Mean	Holotype ♂, BM 7.1.1.428 Malaya	♂, BM 74.455 Malaya	♀, BM 74.456 Malaya	n	Range	Mean
Greatest length of skull	14·2	14·4	25	17·2–19·9	18·9	–	21·4	21·1	4	12·7–13·2	13·0
Condylocanine length	13·2	13·7	29	17·4–19·7	18·5	–	20·3	19·8	5	11·8–12·5	12·1
Condylobasal length	13·3	13·6	28	17·0–19·6	18·2	–	20·2	19·6	5	11·7–12·4	12·0
Length orbit–gnathion	2·8	2·9	30	4·5– 5·2	4·9	5·0	5·4	5·1	5	2·9– 3·2	3·0
Width across anteorbital foramina	–	4·4	31	6·5– 7·9	7·2	7·7	8·1	8·0	6	4·8– 5·3	5·1
Width across front of orbits	5·7	5·8	29	8·9–10·3	9·5	9·9	11·1	10·4	6	5·8– 6·5	6·1
Width across supraorbital swellings	5·0	5·2	28	7·5– 8·8	8·0	9·4	10·1	9·7	5	5·9– 6·3	6·2
Zygomatic width	9·1	–	18	13·3–15·3	14·2	–	15·5	15·2	1	8·7	
Postorbital width	3·9	4·1	30	4·5– 5·4	4·9	6·0	5·8	6·0	6	4·3– 4·7	4·5
Width of braincase	7·5	7·9	26	9·4–10·7	9·9	–	10·7	10·7	6	7·0– 7·5	7·2
Height of braincase	5·6	5·8	27	6·4– 7·1	6·7	–	7·6	7·6	6	4·6– 5·0	4·9
Mastoid width	8·1	8·5	24	10·4–12·1	11·2	–	12·2	12·2	5	7·5– 8·0	7·7
c^1–c^1	4·9	5·1	29	6·1– 7·2	6·6	7·5	8·1	7·8	5	4·0– 4·4	4·2
m^3–m^3	5·9	6·2	30	8·5–10·2	9·3	9·9	10·2	10·1	5	5·9– 6·3	6·1
c–m^3	4·5	4·6	34	7·0– 8·1	7·5	8·2	8·3	7·7	5	4·2– 4·4	4·3
Length of complete mandible	9·0	9·5	24	13·4–15·7	14·5	15·5	15·6	15·2	2	8·5, 9·6	
Length of right ramus	–	10·2	28	13·9–16·1	14·9	16·2	16·3	16·0	5	8·8–10·1	9·2
c–m_3	4·9	5·0	31	7·9– 9·1	8·3	9·3	9·5	8·8	5	4·5– 4·9	4·7

n, number of specimens.

toothrow with a low supporting cusp behind the central one of the three incisive cusps either of i_2 or of i_3. It differs quite sharply from *Chalinolobus* in the presence of a triangular lobule at the base of the posterior margin of the tragus rather than a low convexity; in its broad, saccular rather than smooth, prepuce which has a rounded, slightly V-shaped, preputial orifice and not a narrow vertical aperture; in wide, not narrow, pre-palatal emargination; in the structure of i^3, a simple cusp with broad cingulum rather than a broader, hollowed tooth and in the position of this tooth in the row rather than extruded from it. Despite some similarities, therefore, there appears to be no direct connection between this species and consequently *Hesperoptenus* with either *Glauconycteris* or *Chalinolobus*.

Hesperoptenus doriae differs sufficiently from the other species hitherto assigned to the genus as to justify their separation in a distinct subgenus. For this I propose :

MILITHRONYCTERIS subgen. nov.

TYPE SPECIES. *Nycticejus tickelli* Blyth, 1851.

INCLUDED SPECIES. *Vesperugo* (*Hesperoptenus*) *blanfordi* Dobson, 1877; *Hesperoptenus tomesi* Thomas, 1905.

ETYMOLOGY. The name of this newly separated subgenus has been chosen to commemorate the late G. S. Miller, the monographer of bat genera, at one time of the United States National Museum, now the National Museum of Natural History, Washington. The name is derived from μυλωθρος, a master miller, and νυκτερις, a bat.

DIAGNOSIS. Like *Hesperoptenus* (*Hesperoptenus*) but ears and tragus fleshy rather than membranaceous; second phalange of third digit reduced, its length about equal to or less than the length of the first phalange; braincase lacking any marked inflation, elongate rather than globose; rostrum much broadened supraorbitally; lower maxillary margin of orbit heavy, flange-like, viewed ventrally forming a wide ledge alongside the toothrow; maxillary toothrows convergent anteriorly; and outer upper incisor intruded from toothrow to the extent that on occasion it may lie behind the inner upper incisor.

DESCRIPTION. Similar externally to *Hesperoptenus* (*Hesperoptenus*) but internarial region sometimes densely covered with short hairs; facial warts sometimes low and imperceptible; ear and tragus fleshy, the tip of the tragus sometimes considerably attenuated and prolonged anteriorly.

Skull with uninflated, elongate, slightly broadened braincase; frontal region barely elevated, the cranial profile straight or nearly so; rostrum relatively short, wide, the supraorbital region inflated and swollen; rostral depression very shallow or absent; an almost imperceptible depressed area immediately above the anterior part of the orbit; anteorbital foramen large; lower maxillary margin of orbit wide, flange-like; narial emargination deep, rounded posteriorly; pre-palatal emargination deep, wide, its lateral margins extending beyond the inner faces of the inner upper incisors (i^{1-1}), extending posteriorly to or almost to a line joining the posterior

faces of the upper canines (c^{1-1}) ; post-palatal extension short, wide, with prominent median spine ; shallow but evident basioccipital pits ; bullae of moderate size.

Dentition much as in the nominate subgenus but outer upper incisor (i^3) intruded from toothrow so that the centre of the tooth lies almost exactly behind the centre of the inner upper incisor (i^2), with its anterior face lying approximately on a line joining the anterior faces of the upper canines (c^{1-1}), the tooth in contact or nearly in contact with the posterior face of i^2 and with the antero-internal face of c^1 ; anterior lower premolar (pm_2) about one half or a little less the basal area of the second lower premolar (pm_4), slightly compressed in the toothrow.

DISTRIBUTION. India, Sri Lanka and the Andaman Islands east to Thailand, Malaya and Sabah, Borneo ; possibly occurs also in China.

REMARKS. As here understood, the subgenus *Milithronycteris* includes three species, *tickelli*, *tomesi* and *blanfordi*. The larger species *tickelli* and *tomesi* are clearly more closely related to each other than either is to the very much smaller *blanfordi*, from which they differ quite sharply in a number of features. Nevertheless, in *blanfordi* as in the larger species, the braincase is broad, low and elongate, the rostrum expanded supraorbitally, with a broad sub-orbital flange, and the outer upper incisor (i^3) is intruded to lie behind the inner tooth (i^2). The three species may be keyed :

1 Large, length of forearm 48·6–60·0 mm 2
– Small, length of forearm 25·9–27·5 mm . . . . . ***blanfordi*** (p. 21)
2 Dorsally yellowish brown to straw brown, ventrally a little paler ; anterior dentition to premolars not especially massive ; lower incisors (i_{1-3}) not greatly imbricated ***tickelli*** (p. 15)
– Rich chocolate brown both dorsally and ventrally ; anterior dentition to premolars heavy and massive ; lower incisors (i_{1-3}) much imbricated . . . ***tomesi*** (p. 19)

Hesperoptenus tickelli (Blyth, 1851)

Nycticejus isabellinus Kelaart (ex Blyth), 1850 : 317 (pagination of reprint of 1890). Nomen nudum. Sri Lanka.
Nycticejus tickelli Blyth, 1851 : 157. 'Central India, Ceylon and the intervening hilly country.' Restricted to Chaibassa, Bihar (Anderson, 1881 : 132, Wroughton, 1918 : 593).
Nycticejus isabellinus Horsfield (ex Blyth), 1851 : 38. Central India.
Nycticejus tickelli, Kelaart, 1852 : 24 ; Wagner, 1855 : 765, footnote, 766 ; Blyth, 1863 : 31.
Nycticejus isabellinus, Kelaart, 1852 : 24 ; Wagner, 1855 : 765, footnote ; Fitzinger, 1870 : 363 ; Dobson, 1876 : 113 ; 1878 : 240 ; Blanford, 1891 : 317.
N. [*ycticejus*] *isabellinus*, Blyth, 1863 : 31.
Nycticejus tickellii Fitzinger, 1870 : 362. Lapsus.
Vesperugo (*Vesperus*) *tickelli*, Dobson, 1876 : 104, 113, figs a, b, 208.
Vesperugo (*Hesperoptenus*) *tickelli*, Dobson, 1877 : 312 ; 1878 : 239, 240, pl. 12, fig. 3.
Vesperugo (*Hesperopterus*) (sic) *tickelli*, Anderson, 1881 : 132.
Vesperugo tickelli, Sterndale, 1884 : 63 ; Blanford, 1891 : 317, fig. 97.
Hesperoptenus tickelli, Jentink, 1887 : 278 ; Wroughton, 1897 : 723 ; Trouessart, 1897 : 116 ; 1904 : 83 ; Thomas, 1905 : 575 ; Miller, 1907 : 211 ; Wroughton, 1912 : 1180 ; 1913 : 37 ; 1915a : 86 ; 1915b : 103 ; 1917 : 66 ; 1918 : 593 ; Phillips, 1932a : 345 ; 1932b : 349 ; 1932c : 133 ; 1932d : 137 ; 1933 : 240 ; 1935 : 118 ; Tate, 1942 : 269 ; Ellerman & Morrison-Scott, 1951 : 174 ; Brosset, 1962 : 729 ; Hill, 1967 : 7 ; Hill & Thonglongya, 1972 : 191.

Hesperoptenus tickelii Jentink, 1888 : 182. Lapsus.
[*Hesperoptenus*] *isabellinus*, Trouessart, 1897 : 116.
Hesperoptenus isabellinus, Tate, 1942 : 269.

SYNTYPES. Dobson (1876 : 114 ; 1878 : 241) stated 'Type in the collection of the Indian Museum, Calcutta' but did not designate a specimen. Anderson (1881 : 132) listed as types three specimens in the Indian Museum. These are skins from Cháibasá (= Chaibassa, Bihar, India) presented in 1842 by S. R. Tickell to the Asiatic Society of Bengal, whose Museum later became a part of the Indian Museum. Listed as 156a–c by Anderson (1881 : 132) in the Indian Museum collections, these specimens are numbered 95A–C in Blyth's Catalogue (1863 : 31) of the mammals in the Museum of the Asiatic Society of Bengal and by Dobson (1876 : 208) as 474–476 in a catalogue of the specimens of Chiroptera in the collection of the Indian Museum which he provided in his *Monograph of the Asiatic Chiroptera*. Blyth (1863 : 31) also listed without data a skull (95D) later recorded (as 477) by Dobson (1876 : 208) as having the same data as the three skins, but Anderson (1881 : 132) lists this skull (as 156d) without locality but as originating from S. R. Tickell in 1842.

OTHER TYPE MATERIAL. Horsfield (1851 : 38) lists only a single specimen under *Nycticejus isabellinus*, a dried example from Central India, in the Museum of the Honourable East India Company, presented by the Asiatic Society of Bengal. There is little doubt that this specimen is that now registered as BM 60.5.4.12, presented to the British Museum (Natural History) by the Secretary of State for India, and from the East India House collection. It is a skin with skull in situ, but with the upper incisors visible, labelled in Blyth's handwriting '*Nycticejus isabellinus* Bl. Central India' and by Dobson '*Vesperugo tickelli*, Blyth. Syn. *V. isabellinus*, Blyth'. The specimen is therefore apparently the holotype of *Nycticejus isabellinus* Horsfield, 1851 : it exactly resembles *Hesperoptenus tickelli* as Dobson recognized.

DESCRIPTION. Muzzle much as in *Hesperoptenus doriae*, the longitudinal depressions behind nostrils shallow and faint ; membrane of ear and tragus thick and fleshy, fur extending densely on outer surface of conch for about one half the length of the ear, the inner surface with a few sparse hairs ; anterior margin of ear with a well-developed, slightly pointed posteriorly directed basal lobe ; proximally the anterior margin is strongly convex, distally nearly straight, the tip of the ear broadly rounded, the posterior margin convex. Tragus (Fig. 1c) about one half the length of the ear, slightly hatchet-shaped, widest at about one half its length, its tip narrow, rounded, anteriorly directed, the upper margin nearly horizontal, then sharply convex to join the rather less convex posterior margin.

Thumb relatively long, with a slight sprinkling of short hairs along its dorsal surface and with a strong claw ; forearm naked ; dorsal surface of tibia and foot with a few sparse, short hairs ; fur extending very sparsely on to the dorsal surface of the uropatagium for about one half its width, its ventral surface with a few scattered short hairs ; metacarpals of approximately equal length but the third usually slightly the longest ; post-calcarial lobe linear or slightly rounded at its

central point, lacking a cartilaginous support ; penis saccular, with U-shaped preputial opening.

Dorsally yellowish brown to straw brown, brighter posteriorly than anteriorly, the ventral surface similar but paler. Specimens from Sri Lanka and the Andaman Islands are a little darker than are those from the Indian mainland, and are more reddish brown dorsally, especially posteriorly. They also average a little smaller than those from the mainland. The differences, however, are small and scarcely justify subspecific recognition : in any event, specimens from Thailand are similar to Indian examples in colour but in size to those from Sri Lanka and the Andaman Islands. The differences in size are compared in Table 3.

TABLE 3

Dimensions (in mm) of *Hesperoptenus tickelli* from India, Sri Lanka, the Andaman Islands and Thailand

	Length of forearm					Condylobasal length				
	n	Range	Mean	s.d.	s.e.	n	Range	Mean	s.d.	s.e.
India	15	54·3–60·0	57·13	1·92	0·51	11	18·3–19·6	18·96	0·38	0·12
Sri Lanka	25	49·1–56·8	52·24	1·80	0·36	13	17·0–18·3	17·70	0·42	0·12
Andaman Islands		51·1					18·5			
Thailand	3	52·8–54·2	53·43			3	17·8–18·0	17·90		
	m^3–m^3					c–m^3				
	n	Range	Mean	s.d.	s.e.	n	Range	Mean	s.d.	s.e.
India	12	8·9–10·2	9·60	0·38	0·11	12	7·3–8·1	7·79	0·26	0·08
Sri Lanka	13	8·5– 9·5	9·07	0·28	0·08	17	7·1–7·7	7·38	0·19	0·05
Andaman Islands		8·8, 8·9					7·2, 7·2			
Thailand	3	9·1– 9·3	9·23			3	7·3–7·6	7·40		

n, number of specimens; s.d., standard deviation; s.e., standard error of mean.

Skull (Pl. 3a–c) large, with well-developed sagittal and lambdoidal crests, the braincase broad, uninflated ; postorbital region sharply constricted, its width less than the width across the canines at the alveoli ; supraorbital region considerably expanded, the supraorbital ridges terminating in small inflations ; anterior orbital margin sharply defined, in frontal view sloping slightly inwards ; anteorbital foramen of moderate size, enclosed by a moderate bony bar ; maxillary margin of orbit heavy, flange-like ; zygomata slender ; narial emargination usually V-shaped but with rounded apex, sometimes more or less U-shaped ; post-palatal extension short, with widely based but otherwise narrow median spine. Soft palate (Fig. 2b) with six post-canine ridges, the first two unbroken, remainder curving convexly to the median line, the last small, not reaching laterally to the teeth. Basioccipital pits large, shallow, sharply incised into the basisphenoid.

Baculum (Fig. 3b) with strong upward deflection, its shaft long, nearly parallel-sided, curved upwards at its middle part, its tip unthickened, rounded, shaft slightly narrowed towards the base, the basal part of the baculum expanded to form paired basal flanges, separated above and below by median V-shaped fissures.

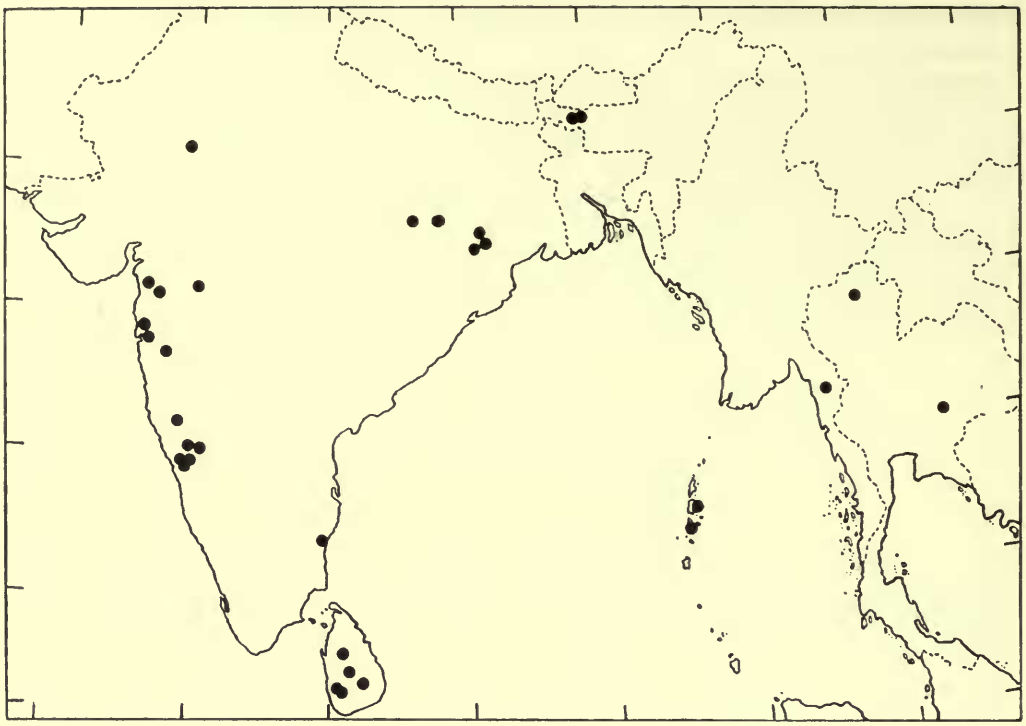

FIG. 4. *Hesperoptenus tickelli*, distribution.

Outer upper incisor (i^3) ovate, with wide, basin-like cingulum and three-faced cusp ; labial part of tooth interposed between inner upper incisor (i^2) and canine (c^1) but tooth otherwise intruded from row, its anterior face in contact with the posterior face of i^2 and lying on or a little in advance of a line joining the anterior faces of c^{1-1}, its postero-lateral face in contact or nearly so with the antero-lateral face of c^1 ; i^2 and c^1 separated by a narrow space equal to or a little less than one half the basal diameter of i^2, the centre of i^3 lying in advance of a line joining the centres of c^{1-1} ; lower incisors (i_{1-3}) thick but linear, not greatly imbricated, i_3 not especially massive (Pls 3a, c, 4e).

Measurements of *Hesperoptenus tickelli* appear in Tables 1 and 2.

DISTRIBUTION (Fig. 4). INDIA (Rajasthan : Dobson, 1878 : 241 ; Blanford, 1891 : 317. Uttar Pradesh : Wroughton, 1913 : 37. West Bengal : Wroughton, 1917 : 66. Bombay, Dobson, 1878 : 241 ; Wroughton, 1897 : 723 ; Brosset, 1962 : 729. Madhya Pradesh : Dobson, 1876 : 114, 208 ; Anderson, 1881 : 132, 133 ; Sterndale, 1884 : 63. Bihar : Dobson, 1876 : 114, 208 ; Anderson, 1881 : 132 ; Sterndale, 1884 : 63 ; Wroughton, 1915b : 103. Madras, Wroughton, 1918 : 593. Mysore : Wroughton, 1912 : 1180. Andaman Islands : Dobson, 1876 : 208 ; Anderson, 1881 : 132 ; Hill, 1967 : 7). SRI LANKA (Kelaart, 1850 : 317 (separate pagination) ; 1852 : 24 ; Blyth, 1863 : 31 ; Dobson, 1878 : 241 ; Wroughton, 1915a : 86 ; Phillips, 1932a : 345 ; 1932b : 349 ; 1932c : 133 ; 1932d : 137 ; 1933 : 240 ; 1935 :

118). BURMA (Dobson, 1877 : 312 ; Anderson, 1881 : 133 ; Blanford, 1891 : 317). THAILAND (Hill & Thonglongya, 1972 : 191). CHINA (Jentink, 1887 : 278 ; 1888 : 182, from 'Kolongsu', not traced).

REMARKS. *Nycticejus isabellinus* Horsfield, 1851. Initially a manuscript name from Blyth, *isabellinus* is validated by Horsfield (1851 : 38) (contrary to the assertion by Blanford, 1891 : 317, who says of this citation 'no description') with the remark 'Of the size of *N. temminckii* [= *Scotophilus kuhlii*], clearly characterised by an uniform isabellina tint both above and underneath'. The earliest use of *isabellinus*, by Kelaart (1850 : 317, pagination from a reprint dated 1890, in the British Museum (Natural History), differing apparently from the original), is without description in a Catalogue of mammals from Sri Lanka. Kelaart (1852 : 24) and Blyth (1863 : 31) list it as a synonym of *tickelli*, as does Fitzinger (1870 : 362), Dobson (1876 : 113 ; 1878 : 240), Blanford (1891 : 317) and Trouessart (1897 : 116). Tate (1942 : 269) listed it in parentheses as [*Hesperoptenus isabellinus* (Horsfield)] and repeated the description by Horsfield.

The names *Nycticejus tickelli* Blyth and *Nycticejus isabellinus* Horsfield both appeared in 1851. In neither of the publications concerned, the *Journal of the Asiatic Society of Bengal* or Horsfield's *Catalogue of the Mammalia in the Museum of the Hon. East-India Company* does there appear evidence to establish a definite date of publication. All that can be said is that the latter certainly appeared after 18 August 1851, the date of its prefatory list of contributors to the Museum ; Blyth's description is in the second issue of the four of the Journal for that year and probably appeared before the account by Horsfield. In these circumstances the name adopted is that employed by the first reviewer, namely Dobson (1876 : 113) ; Fitzinger (1870 : 362) gave a detailed description of the species and might be considered a prior reviewer.

Hesperoptenus tomesi Thomas, 1905

Hesperoptenus tomesi Thomas, 1905 : 575. Malacca, Malaya.
Hesperoptenus tomesi, Kloss, 1908 : 158 ; Chasen, 1940 : 53 ; Tate, 1942 : 269 ; Medway, 1969 : 38 ; Hill, 1972 : 38.
Hesperoptenus doriae, Davis, 1962 : 42 ; Medway, 1965 : 65.

HOLOTYPE. Adult male BM 7.1.1.428. Skin and skull, rear and lower part of cranium missing. From the Tomes Collection.

DIAGNOSIS. Muzzle a little more densely haired than in *H. tickelli* ; tragus (Fig. 1d) slightly more acutely pointed and directed a little further anteriorly ; differs sharply in rich, dark chocolate brown coloration both above and below ; skull larger with more prominent supraorbital ridges terminating in small tubercles ; anterior orbital margin more nearly vertical ; zygomata more widely expanded ; cingulum of outer upper incisor (i^3) a little narrower, tooth further intruded from row and only a little interposed between the inner upper incisor (i^2) and the canine (c^1).

DESCRIPTION. Apart from colour the external features of *H. tomesi* resemble those of *H. tickelli* very closely ; the metacarpals are a little more graduated, with

the third the longest, the fourth usually a little shorter, and the fifth the shortest, although the differences in length are small. The post-calcarial lobe has a rounded central part but is otherwise linear, and lacks a cartilaginous supporting prop; the thumb, forearm and tibia are naked or nearly so.

Skull (Pl. 3d–f) similar to that of *H. tickelli* but braincase a little more elevated, especially posteriorly, with a more pronounced occipital 'helmet'; postorbital region narrow, its width less than the width across the upper canines (c^{1-1}) at the alveoli; anterior orbital margin heavy, flange-like, more sharply defined than in *tickelli*; anteorbital foramen large, closed by a strong flange of bone; zygomata relatively massive anteriorly, heavier than in *tickelli*; narial emargination wide, more or less U-shaped; soft palate (Fig. 2c) much as in *tickelli*; broad post-palatal spine; basioccipital pits a little deeper than in *tickelli*.

Baculum (Fig. 3c) long, with slender, cylindrical shaft, lacking any upward curvature or deflection, tip slightly thickened vertically, upper surface of shaft flattened proximally, the base widened to form paired basal flanges separated by a deep V-shaped aperture. The baculum is longer than in *H. tickelli* and differs in its lack of upward curvature and in narrower basal flanges which are more widely separated.

Inner upper incisor (i^2) relatively larger than in *H. tickelli*; outer upper incisor (i^3) more or less triangular in basal outline, intruded from the toothrow to lie directly behind i^2, its anterior face in contact with the posterior face of that tooth and lying behind a line joining the anterior faces of the canines (c^{1-1}), the tip of its roughly triangular base interposed between the postero-lateral face of i^2 and the antero-lateral face of c^1; centres of i^{3-3} lying on a line joining the centres of c^{1-1}, with i^2 and c^1 almost in contact labially. Remaining dentition much as in *tickelli* but third upper molar (m^3) a little further flattened and platelet-like, its second and third commissures more reduced; lower incisors (i_{1-3}) much imbricated, relatively more massive than in *tickelli*, i_2 with small posterior cingulum cusp behind central cusp, i_3 much thickened, with massive crown in which individual cusps are obscured but with prominent anterior and posterior cingulum cusps, its lateral diameter less than its diameter from front to back. In general, the dentition is considerably heavier than in *tickelli* (Pls 3d, f, 4f).

Measurements of *Hesperoptenus tomesi* are given in Tables 1 and 2.

Distribution. Malaya (Malacca; also two examples from an unknown Malayan locality); Borneo (Sabah).

Remarks. Davis (1962 : 42) recorded as *Hesperoptenus doriae* a specimen from the Sapagaya Forest Reserve, Sandakan, Sabah, Borneo (5°37′N 118°04′E). Through the kindness of Dr J. C. Moore, lately of the Field Museum of Natural History, Chicago, I have been able to examine this specimen, now Field Museum 77025, collected by D. D. Davis on 29 July 1950. As Davis pointed out, it is a juvenile male, but is, however, much larger than the adult holotype of *doriae*, with length of forearm 42·8 mm and $c–m^3$ 7·3 mm, and, although badly damaged with much of the cranium lost, the skull agrees closely with that of *tomesi* to which the specimen must be referred. It is thus the first of the species to be reported from

Borneo. The specimen differs slightly from the Malayan holotype of *tomesi* in the positional relationship of the upper incisors, the outer tooth (i^3) being a little less intruded from the toothrow, with the inner upper incisor (i^2) and the canine (c^1) separated by a slightly wider interspace. A brief account of this specimen can be found in Hill (1972 : 38).

Hesperoptenus tomesi is clearly separated from *H. tickelli* by differences in coloration, cranial architecture, baculum and dentition. That it represents a distinct species cannot be doubted, as Tate (1942 : 268) pointed out from a consideration of the anterior part of the orbit in *tickelli* and *tomesi*. The unique features of the species were first recognized by Tomes who has labelled the holotype '*V. dedalion* n. s.', a circumstance remarked by Thomas (1905 : 576) who would have used the name suggested by Tomes had it matched euphoniously with the generic epithet *Hesperoptenus*.

Hesperoptenus blanfordi (Dobson, 1877)

Vesperugo (*Hesperoptenus*) *blanfordi* Dobson, 1877 : 312. Tenasserim.
Vesperugo (*Hesperoptenus*) *blanfordi*, Dobson, 1878 : 242.
Vesperugo blanfordi, Anderson, 1881 : 133 ; Blanford, 1891 : 317.
Hesperoptenus blanfordi, Jentink, 1888 : 182 ; Trouessart, 1897 : 116 ; 1904 : 83 ; Miller, 1907 : 211 ; Kloss, 1908 : 158 ; Robinson & Kloss, 1915 : 116 ; Thomas, 1916 : 2 ; Wroughton, 1918 : 393 ; Gyldenstolpe, 1919 : 137 ; Chasen, 1940 : 52 ; Tate, 1942 : 270 ; Ellerman & Morrison-Scott, 1951 : 174 ; Medway, 1969 : 38 ; Hill, 1972 : 37 ; Hill & Thonglongya, 1972 : 191.

Holotype. Adult male No. 157a in the Indian Museum, Calcutta. In alcohol. Presented by W. T. Blanford.

Type locality. The holotype is said by Blanford (1891 : 318) to have been obtained east of Moulmein in Burma.

Diagnosis. Much smaller than *H. tickelli* or *H. tomesi* ; internarial region densely haired ; tragus (Fig. 1e) less acutely pointed ; facial warts imperceptible; upper surface of forearm densely haired ; a broad, cushion-like pad at base of thumb ; braincase flattened ; postorbital region relatively much wider ; outer upper incisor (i^3) greatly reduced ; third molars ($m \frac{3}{3}$) more reduced.

Description. Muzzle very low, wide, moderately furred, nostrils semi-lunate, opening sublaterally, no perceptible grooves behind each nostril ; internarial region densely clothed with short hairs to lower edge of nostrils ; lower lip naked except for a few sparse hairs ; a prominent naked area beneath the symphysis menti preceding a low or almost imperceptible wart ; facial warts almost imperceptible or absent ; ear nearly subquadrate but rather more triangular than in *H. tickelli* or *H. tomesi*, its anterior margin strongly convex proximally, with well-developed, roundly pointed basal lobe, distally nearly straight to broadly rounded tip ; posterior margin of ear slightly convex in its distal third, its lower part similarly convex but with a shallow central concavity ; antitragal lobe thickened ; a low, barely perceptible wart, with a few longer hairs, just above the junction of the posterior margin of the ear with the side of the head ; outer surface of conch furred for about one third

of its length, a few sparse hairs internally. Tragus (Fig. 1e) slightly hatchet-shaped, the inner margin sharply concave to a rounded, anteriorly directed tip, upper margin nearly horizontal, posterior margin straight or slightly convex, with a large triangular lobe at its base.

Thumb very short with strong claw, the upper surface of the thumb clothed with short hairs ; a broad, well-developed pad or cushion extending over the base of the thumb and of the second metacarpal ; third and fourth metacarpals usually subequal, fifth a little shorter ; upper surface of forearm densely clothed with fine, short hairs ; upper surface of tibia naked ; feet very small, the sole thickened, a few sparse hairs on the digits ; prominent, rounded post-calcarial lobe supported by a supplementary cartilaginous calcarial spur. No male example in alcohol is available but Dobson (1877 : 313) states that the penis of the holotype resembles that of *H. tickelli*. Dorsal surface bright chestnut brown, ventral surface similar in colour.

Skull (Pl. 4a–c) very small, braincase flattened, wide, with lambdoid ridges but no sagittal crest ; frontal region barely elevated, the cranial profile almost straight ; postorbital region wide, its width exceeding the width across the canines at the alveoli ; a trace only of supraorbital ridges ; slightly inflated lateral rostral swellings with small supraorbital tubercles ; a shallow median rostral depression ; narial emargination deep, extending posteriorly to a line joining the posterior margins of the anteorbital foramina, U-shaped ; anteorbital foramen large, enclosed by a narrow bar ; zygomata slender ; lower maxillary margin of orbit flange-like ; pre-palatal emargination wide anteriorly, its lateral margins extending beyond the inner faces of the inner upper incisors (i^{2-2}), the emargination extending posteriorly almost to a line joining the posterior faces of the canines (c^{1-1}) ; posterior edge of the emargination sometimes with a narrow tongue-like extension into the palate, on occasion extending as far as a line joining the mesostyles of the first upper molars (m^{1-1}). Soft palate (Fig. 2d) with six post-canine ridges, the first straight, unbroken, the second slightly curved, narrowly separated, remainder curved, medianly divided, the last small. Post-palatal extension short, wide, with prominent, broad post-palatal spine ; shallow basioccipital pits not excised sharply into the basisphenoid, separated by a broad ridge.

Upper incisive dentition similar to that of *H. tomesi* but outer incisor (i^3) very small, sometimes minute, one quarter or less the basal area of the inner tooth (i^2), with prominent cingulum and small central cusp, intruded to lie directly behind i^2, its anterior face in contact with the posterior face of that tooth, its outer face in contact with the inner face of the canine (c^1), i^2 and c^1 barely separated. Upper premolar (pm^4) not compressed in the toothrow, its length and width almost equal ; third upper molar (m^3) less than one half the crown area of first upper molar (m^1), with small metacone and much reduced second and third commissures ; lower incisors (i_{1-3}) linear, only slightly if at all imbricated, i_3 a little more massive than i_{1-2} ; anterior lower premolar (pm_2) small, its crown area about one quarter that of the second lower premolar (pm_4), rather compressed in the toothrow ; posterior triangle of third lower molar (m_3) much reduced, the hypoconid small, the entoconid almost obsolete, the posterior part of the tooth about one quarter to one third the area of the anterior triangle (Pl. 4a, c, g).

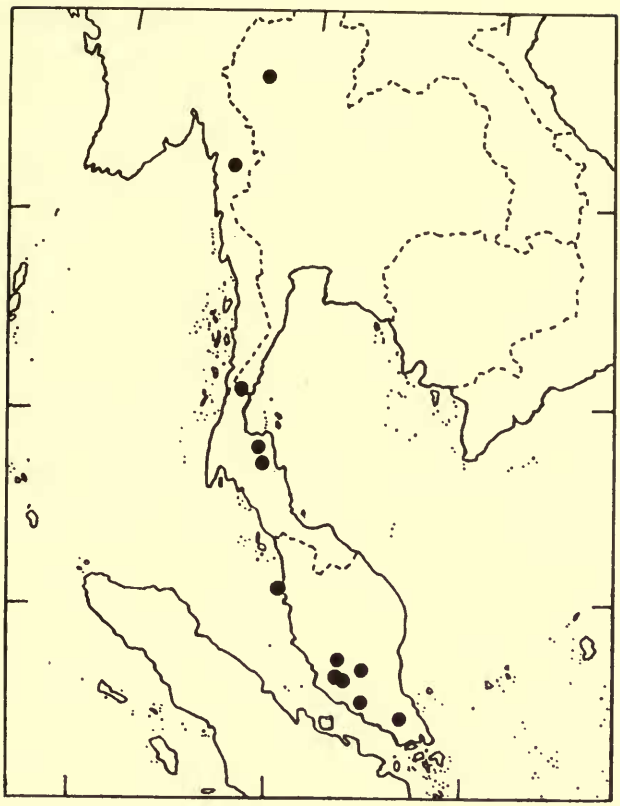

FIG. 5. *Hesperoptenus blanfordi*, distribution.

Measurements of *H. blanfordi* appear in Tables 1 and 2.

DISTRIBUTION (Fig. 5). BURMA (Dobson, 1877 : 312 ; 1878 : 242 ; Anderson, 1881 : 133 ; Blanford, 1891 : 318) ; THAILAND (Jentink, 1888 : 182 (Jongo Hills, perhaps = Chongo Hills, 10°17'N 99°01'E) ; Robinson & Kloss, 1915 : 116 ; Thomas, 1916 : 2 ; Gyldenstolpe, 1919 : 137 ; Hill & Thonglongya, 1972 : 191); MALAYA (Anderson, 1881 : 133 ; Blanford, 1891 : 318 ; Thomas, 1916 : 2 ; Hill, 1972 : 37).

REMARKS. Flattening and broadening of the braincase, with a wide postorbital region and rostrum, is characteristic of the vespertilionine genera *Tylonycteris* and *Mimetillus*, which also have pads on the thumbs and feet. In these, however, the braincase is yet more flattened than in *H. blanfordi* and no extensive shortening of the rostrum has occurred. Rostral inflation in *H. blanfordi* is of the same order as that in *Tylonycteris*, with the supraorbital area swollen to develop sometimes a small tubercle. In *Mimetillus* the whole of this area is inflated, together with the upper part of the bar enclosing the anteorbital foramen and the region immediately above this aperture, but with no definite tubercle. Although *Tylonycteris* and *Mimetillus* have the same dental formula as *Hesperoptenus*, the inner upper incisor (i^2) is bicuspid and the outer upper incisor (i^3) remains in the toothrow, separated from the canine

by a small interspace. Further, in *Mimetillus* the wing is much reduced by shortening of the third and fifth digits ; in *H. blanfordi* the digits are not reduced and indeed are relatively rather long.

Of other vespertilionine bats with pads on thumbs and feet, *Eudiscopus denticulus* has an extreme degree of flattening of the skull with uninflated, unshortened, rostrum and retains the anteriormost upper premolar (pm^2) with a minute second lower premolar (pm_3) intruded between the anterior (pm_2) and posterior (pm_4) lower premolars. The braincase is higher in *Myotis rosseti* which has a caniniform outer upper incisor (i^3) exceeding the inner tooth (i^2) in basal area and which also retains the anteriormost upper premolar (pm^2) ; *Glischropus tylopus* cranially is like *Pipistrellus*, with the rostrum unexpanded and not much shortened although i^3 is extruded to lie alongside i^2, the four incisors forming a straight line, and with pm^2 present and retained in the toothrow. In all of these, i^2 remains rather elongate as it is in *Tylonycteris* and *Mimetillus*, and is similarly bicuspid. The massive, unicuspid i^2 and displaced i^3 ally *blanfordi* with *H. tickelli* and *H. tomesi* which it almost exactly resembles in the features of its upper incisive dentition although in a number of other features it differs quite sharply from either of these species.

RELATIONSHIPS

It is clear that *Hesperoptenus* as here understood embodies two rather widely separated trends, one represented by a single species (*doriae*), the other by three (*tickelli*, *tomesi* and *blanfordi*). At the same time, one species of the latter group (*blanfordi*) is quite sharply removed from its associates and apparently represents a further course of adaptation.

Thomas (1902 : 220) thought *Hesperoptenus* related to *Philetor* but apart from any other considerations the upper incisors of *Philetor* differ widely, the inner tooth (i^2) being elongate, long and bicuspid, with the outer tooth (i^3) not displaced. Indeed, *Philetor* is closely related to *Pipistrellus* (Hill, 1966 : 380 ; 1971 : 143). Miller (1907 : 211) compared the dentition of *Hesperoptenus* with *Eptesicus* and *Vespertilio* but examined only *tickelli*, and Tate (1942 : 232, 233, 268) included the genus among the 'pipistrelloid' genera. Tate added (p. 269) that in *tickelli* (he did not examine either *doriae* or *blanfordi*) the upper incisors show an interesting intermediate condition between the *Pipistrellus*-like genera which have mostly a bicuspid inner tooth (i^2), with the outer tooth (i^3) present, and the *Scotophilus*-like genera in which i^2 is unicuspid and i^3 is lost. In *doriae*, *tickelli*, *tomesi* and *blanfordi* i^2 is massive and unicuspid and in all but the first of these i^3 is markedly displaced inwardly from the toothrow, this feature reaching an extreme in *tomesi* and *blanfordi*. *Hesperoptenus doriae* indeed stands nearest to the pipistrelline genera and has a number of similarities to *Glauconycteris* and, to a lesser extent, to *Chalinolobus*. Its braincase is rather inflated, its rostrum not much shortened or broadened to the extent that it is in *tickelli*, *tomesi* or *blanfordi*, and its outer upper incisors are not greatly displaced as they are in its congeners. It is therefore considered the least modified member of *Hesperoptenus*.

The remaining species *tickelli*, *tomesi* and *blanfordi* in many ways approach the 'nycticeine' genera (Tate, 1942 : 280) allied to *Scotophilus*, and, indeed, in these the

elongated braincase and greatly broadened rostrum are features strongly reminiscent of that genus or of *Scotomanes*. The large species *tickelli* and *tomesi* are similar to *Scotophilus* in the general appearance of the head and ears and also in the shape of the tragus, which is widened to some extent at its centre, rather than elongate and more or less spatulate as in the pipistrelline genera. In fact, the early authors referred *tickelli* to *Nycticejus* (in part = *Scotophilus*) and, on occasion, even relatively modern specimens referred by previous identifiers to *Hesperoptenus* have been found to be examples of *Scotophilus*.

The nycticeine genera are characterized among other features by the unicuspid inner upper incisor (i^2) and by the loss of the outer upper incisor (i^3) and of the small anteriormost upper premolar (pm^2) although at the base of their sequence a rudimentary i^3 is sometimes present in *Scotozous* which also retains pm^2; the latter tooth also occurs sometimes in *Scotoecus*. *Scotozous* has been thought to be pipistrelline rather than nycticeine (Tate, 1942 : 259) but, if the African *rueppellii* is excluded, then, as Tate (p. 260) postulated, the genus with its remaining Indian species *dormeri* is transitional between *Pipistrellus* and the nycticeine genera in which i^3 and pm^2 are lost. In *Hesperoptenus*, contrary to the usual nycticeine condition, i^3 is present and furthermore usually well developed. However, shortening of the rostrum has led to its intrusion from the toothrow in three of four species, and, as in most nycticeines, pm^2 has been lost. It is effectively further separated from *Scotophilus* by the lack of any distortion of the W-pattern of the first and second upper molars (m^{1-2}) and from *Scotomanes* by its less widely expanded rostrum, the anterior orbital margin not swollen or beaded (although the flange-like margin of *tomesi* tends towards this condition), and its lack of a pronounced rostral depression.

Hesperoptenus provides, therefore, a further example of a tendency apparent among some Vespertilionidae to shorten and broaden the rostrum with concomitant reduction of the dentition, in some by the loss of the outer upper incisor (i^3) with consequent enlargement of the inner upper incisor (i^2), the loss of the anterior upper premolar (pm^2), and some reduction of the third upper molar (m^3). The process has not progressed as far in *Hesperoptenus* as in the genera most modified in these respects and, indeed, has taken a different course, with the removal of i^3 from the toothrow rather than its loss. One species (*doriae*) remains relatively unmodified, and one (*blanfordi*) has clearly diverged rather widely with further modification of the skull and with the development of pads on the thumbs. The latter, however, occur quite independently in various sections of the Vespertilioninae, in the 'myotine' type in *Eudiscopus* and *Myotis*, the 'pipistrelline' type in *Glischropus*, *Tylonycteris* and *Mimetillus*, and in *blanfordi* in a species that in many ways approaches the 'nycticeine' type. The conclusion seems unavoidable that *Hesperoptenus* must be placed with the genera *Scotozous*, *Scotoecus* and *Nycticeius* that link the more truly pipistrelline bats to the more modified, extreme nycticeine bats such as *Scotomanes* and *Scotophilus*.

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REFERENCES

Anderson, J. 1881. *Catalogue of Mammalia in the Indian Museum, Calcutta.* Calcutta.

Blanford, W. T. 1891. *The Fauna of British India including Ceylon and Burma. Mammalia.* Part II. London.

Blyth, E. 1851. Report on the Mammalia and more remarkable species of birds inhabiting Ceylon. *J. Asiat. Soc. Beng.* **20** : 153–185.

—— 1863. *Catalogue of the Mammalia in the Museum of the Asiatic Society of Bengal.* Calcutta.

Brosset, A. 1962. The bats of central and western India. Part II. *J. Bombay nat. Hist. Soc.* **59** : 583-624, 4 pls, 9 maps.

Chasen, F. N. 1940. A handlist of Malaysian mammals. *Bull. Raffles Mus.* No. 15 : i–xx, 1–209, map.

Davis, D. D. 1962. Mammals of the lowland rain-forest of North Borneo. *Bull. natn. Mus. St. Singapore*, No. 31 : 1–129, 20 figs, 23 pls.

Dobson, G. E. 1876. *Monograph of the Asiatic Chiroptera and Catalogue of the species of bats in the Collection of the Indian Museum, Calcutta.* London.

—— 1877. Notes on a collection of Chiroptera from India and Burma, with descriptions of new species. *J. Asiat. Soc. Beng.* **46**, (2) : 310–313.

—— 1878. *Catalogue of the Chiroptera in the Collection of the British Museum.* London.

—— 1880. Report on accessions to our knowledge of the Chiroptera during the past two years (1878–80). *Report of the British Association* 169–197.

Ellerman, J. R. & Morrison-Scott, T. C. S. 1951. *Checklist of Palaearctic and Indian mammals, 1758–1946.* London.

Fitzinger, L. J. 1870. Kritische Durchsicht der Ordnung der Flatterthiere oder Handflügler (Chiroptera). Familie der Fledermäuse (Vespertiliones). V. Abtheilung. *Sber. Akad Wiss. Wien* **62**, (1) : 353–438.

Gyldenstolpe, N. 1919. A list of the mammals at present known to inhabit Siam. *J. nat. Hist. Soc. Siam* **3**, (3) : 127–175.

Hill, J. E. 1966. A review of the genus *Philetor* (Chiroptera :Vespertilionidae). *Bull. Br. Mus. nat. Hist.* (Zool.) **14** : 373–382, 3 figs.

—— 1967. The bats of the Andaman and Nicobar Islands. *J. Bombay nat. Hist. Soc.* **64** : 1–9.

—— 1971. The status of *Vespertilio brachypterus* Temminck (Chiroptera : Vespertilionidae). *Zool. Meded. Leiden* **45** : 141–146.

—— 1972. New records of Malayan bats, with taxonomic notes and the description of a new *Pipistrellus*. *Bull. Br. Mus. nat. Hist.* (Zool.) **23** : 21–42, 3 tabs.

—— & Thonglongya, K. 1972. Bats from Thailand and Cambodia. *Bull. Br. Mus. nat. Hist.* (Zool.) **22** : 171–196, 4 figs, 2 tabs.

Horsfield, T. 1851. *A Catalogue of the Mammalia in the Museum of the Hon. East-India Company.* London.

Hose, C. 1893. *A descriptive account of the mammals of Borneo.* London.

Jentink, F. A. 1887. *In* Schlegel, H. & Jentink, F. A. *Muséum d'Histoire Naturelle des Pays-Bas. Revue méthodique et critique des Collections déposées dans cet Etablissement. Tome 10. Catalogue Ostéologique des mammifères.* Leiden.

JENTINK, F. A. 1888. *In* Schlegel, H. & Jentink, F. A. *Muséum d'Histoire Naturelle des Pays-Bas. Revue méthodique et critique des Collections déposées dans cet Etablissement. Tome 12. Catalogue Systématique des mammifères* (*Rongeurs, Insectivores, Cheiroptères, Edentés et Marsupiaux*). Leiden.

KELAART, E. F. 1850. List of Mammalia observed or collected in Ceylon. *Jl R. Asiat. Soc. Ceylon* **2** (2) : 316–320 (pagination from reprint of 1890).

—— 1852. *Prodromus Faunae Zeylanicae : being contributions to the Zoology of Ceylon.* Colombo.

KLOSS, C. B. 1908. A list of the bats occurring in the Peninsular Region with a key to the genera. *J. fed. Malay St. Mus.* **2** : 151–161.

KOOPMAN, K. F. 1971. Taxonomic notes on *Chalinolobus* and *Glauconycteris* (Chiroptera, Vespertilionidae). *Am. Mus. Novit.* No. 2451 : 1–10, 1 fig.

MEDWAY, LORD. 1965. Mammals of Borneo. Field keys and an annotated checklist. *J. Malay. Brch R. Asiat. Soc.* (1963), **36** : i–xiv, 1–193, 9 figs, 34 pls, 5 tabs, map.

—— 1969. *The wild mammals of Malaya and offshore Islands including Singapore.* Kuala Lumpur ; London.

MILLER, G. S. 1907. The families and genera of bats. *Bull. U.S. natn. Mus.* **57** : i–xvii, 1–282, 49 figs, 14 pls.

PETERS, W. 1869a. Mittheilung über die von dem Hon. Marquis Giacomo Doria in Sarawak auf Borneo gesammelten Flederthiere. *Mber. K. preuss. Akad. Wiss.* (1868) : 626–627.

—— 1869b. Mittheilung über neue Säugethiere (*Colobus, Rhinolophus, Vesperus*) und neue oder weniger bekannte Amphibien (*Hemidactylus, Herpetodryas, Spilotes, Elaphis, Lamprophis, Erythrolamprus*). *Mber. K. preuss. Akad. Wiss.* (1868) : 637–643.

—— 1906. *Chiroptera of Berlin Museum.* Berlin

PETERSON, R. L. & SMITH, D. A. 1973. A new species of *Glauconycteris* (Vespertilionidae, Chiroptera). *Life Sci. Occ. Pap. R. Ont. Mus.* No. 22 : 1–9, 4 figs.

PHILLIPS, W. W. A. 1932a. Survey of the distribution of mammals in Ceylon. Report No. 2. *Ceylon J. Sci.* B, **16** : 341–347.

—— 1932b. Survey of the distribution of mammals in Ceylon. Report No. 3. *Ceylon J. Sci.* B, **16** : 347–351.

—— 1932c. Survey of the distribution of mammals in Ceylon. Report No. 5. *Ceylon J. Sci.* B, **17** : 131–134.

—— 1932d. Survey of the distribution of mammals in Ceylon. Report No. 7. *Ceylon J. Sci.* B, **17** : 136–138.

—— 1933. Survey of the distribution of mammals in Ceylon. Report No. 8. *Ceylon J. Sci.* B, **17** : 237–242.

—— 1935. *Manual of the mammals of Ceylon.* Colombo.

ROBINSON, H. C. & KLOSS, C. B. 1915. On a collection of mammals from the Siamese Province of Bandon, N. E. Malay Peninsula. *J. fed. Malay St. Mus.* **5** : 111–127.

ROSEVEAR, D. R. 1965. *The bats of West Africa.* London.

RYAN, R. M. 1966. A new and some imperfectly known Australian *Chalinolobus* and the taxonomic status of African *Glauconycteris*. *J. Mammal.* **47** : 86–91, 1 tab.

STERNDALE, R. A. 1884. *Natural History of the Mammalia of India and Ceylon.* Calcutta.

TATE, G. H. H. 1942. Review of the vespertilionine bats, with special attention to genera and species of the Archbold Collections. *Bull. Am. Mus. nat. Hist.* **80** : 221–297, 5 figs.

THOMAS, O. 1902. On a new genus of vespertilionine bat from New Guinea. *Ann. Mag. nat. Hist.* (7), **9** : 220–222.

—— 1905. A new genus and two new species of bats. *Ann. Mag. nat. Hist.* (7), **16** : 572–576.

—— 1913. On some specimens of *Glauconycteris* from the Cameroons. *Ann. Mag. nat. Hist.* (8), **11** : 144–145.

—— 1916. List of Microchiroptera, other than leaf-nose bats, in the collection of the Federated Malay States Museums. *J. fed. Malay St. Mus.* **7** : 1–6.

TROUESSART, E-L. 1897. *Catalogus mammalium tam viventium quam fossilium. I. Primates, Prosimiae, Chiroptera, Insectivora, Carnivora, Rodentia, Pinnipedia.* Berlin.

TROUESSART, E-L. 1904. *Catalogus mammalium tam viventium quam fossilium. Quinquennale supplementum.* Berlin.

WAGNER, J. A. 1855. *Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen von Dr. Johann Christian Daniel von Schreber.* Supplementband 5. Leipzig.

WROUGHTON, R. C. 1897. Some Konkan bats. *J. Bombay nat. Hist. Soc.* **12** : 716–725, 1 pl.

—— 1912. Bombay Natural History Society's Mammal Survey of India. No. 5. Dharwar. *J. Bombay nat. Hist. Soc.* **21** : 1170–1195.

—— 1913. Bombay Natural History Society's Mammal Survey of India. No. 6. Kanara. *J. Bombay nat. Hist. Soc.* **22** : 29–44.

—— 1915a. Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon. Report No. 18. Ceylon. *J. Bombay nat. Hist. Soc.* **24** : 79–96.

—— 1915b. Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon. Report No. 19. Bengal, Bihar and Orissa. *J. Bombay nat. Hist. Soc.* **24** : 96–110.

—— 1917. Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon. Report No. 27. Bhutan Duars. *J. Bombay nat. Hist. Soc.* **25** : 62–71.

—— 1918. Summary of the results from the Indian Mammal Survey of the Bombay Natural History Society. *J. Bombay nat. Hist. Soc.* **25** : 547–598.

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